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Diversity patterns of native and exotic fish species suggest homogenization processes, but partly fail to highlight extinction threats

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Abstract

Aim: Exotic species are a major threat to biodiversity and have modified native communities worldwide. Invasion processes have been extensively studied, but studies on species richness and beta diversity patterns of exotic and native species are rare. We investigate such patterns among exotic and native fish communities in upland and lowland rivers to explore their relationship with environmental drivers.

Location: Northern Italy.

Methods: Exotic and native fish beta diversity patterns were investigated separately in lowland and upland sites using Local Contribution to Beta Diversity (LCBD) and Species Contribution to Beta Diversity (SCBD) analyses. To examine the main environmental variables affecting the LCBD, a Boosted Regression Trees (BRT) method was used. Community dispersion among and within stream orders was investigated with the PERMDISP test.

Results: In lowland sites, exotic species richness was higher than native species richness, especially in large rivers and drainage canals. An opposite trend was found in upland sites, where native species richness was higher than exotic species richness, especially in large rivers. No clear LCBD patterns were found along stream orders in the lowland, whereas higher stream orders in the upland showed the highest LCBD. Its patterns in upland and lowland sites were related to a number of factors, such as total suspended solids and total phosphorus. Community dispersion among stream orders did not show a relationship with environmental heterogeneity. SCBD values were positively correlated with species occupancy in the study area, and native species showed higher SCBD values than exotic species only in the uplands.

Main conclusions: Large rivers in the uplands are important in maintaining native fish diversity and should be protected against invasive fish. In contrast, most lowland rivers have suffered from biological homogenization. Some rare native species can show low contribution to beta diversity, but still need conservation actions due to their risk of local extinction.

KEYWORDS
Alien species, beta diversity, biodiversity conservation, freshwater, invasions, non-native species, species diversity, species richness

1 | INTRODUCTION

The importance of biodiversity for ecosystem functioning and resilience, as well as for humans through the supply of ecosystem services (e.g., food, pest control, fisheries), is widely acknowledged (Cardinale et al., 2012; Hooper et al., 2005; Worm et al., 2006). Nevertheless, biodiversity constantly declines worldwide (Butchart et al., 2010) and to define management plans that can halt this decline it is necessary to understand biodiversity trends in space and time (Richardson & Whittaker, 2010). A common approach to detect these biodiversity trends is to measure variations in taxonomical diversity (Chiarucci, Bacaro, & Scheiner, 2011; Colwell & Coddington, 1994). In 1960, Whittaker proposed the taxonomical diversity could be defined as the result of three components: alpha (local diversity), beta (variation of community composition among sites) and gamma diversity (regional diversity; Whittaker, 1960, 1972). In recent years, more attention has been focused on beta diversity (Anderson et al., 2011) due to its ability to identify human impacts on diversity (e.g., agriculture, species invasion and climate change) at multiple scales (Socolar, Gilroy, Kunin, & Edwards, 2016). Different measures of beta diversity have been proposed (e.g., Baselga, 2010; Tuomisto, 2010), and recently, Legendre and De Cáceres (2013) proposed a method that not only estimates the overall beta diversity, but also quantifies the Local Contribution to Beta Diversity (LCBD) by single sites and the Species Contribution to Beta Diversity (SCBD) by individual species. Both LCBD and SCBD can also be considered as measures of the uniqueness of sites and species for a region and have been used to investigate species distribution shifts in fish communities (Kuczynski, Legendre, & Grenouillet, 2017) and other taxa such as diatom communities (Jyrkänkallio-Mikkola, Siljander, Heikinheimo, Pellikka, & Soininen, 2018) and stream invertebrates (Heino & Grönroos, 2017; Sor, Legendre, & Lek, 2018; Tonkin, Heino, Sundermann, Haase, & Jähnig, 2016).

Despite the importance of diversity measures in explaining taxonomical biodiversity, the main shortcoming of these measures is that all species are typically considered equally, without taking into account evolutionary or ecological differences between species (Chiarucci et al., 2011). For example, taking into account the native or exotic status of a species has important implications in terms of management and conservation, also considering that the invasion sensitivity of the community could be related to diversity measures such as species richness (Hooper et al., 2005). Invasions of exotic species can often cause a native species' decline through predation, hybridization, competition and indirect effects (Blackburn et al., 2014; Simberloff et al., 2013).

Freshwaters are particularly susceptible to exotic species invasions, and in such ecosystems, exotic species are considered one of the main causes of biodiversity loss (Dudgeon et al., 2006). For instance, in fish communities, exotic species constitute one of the major drivers of extinction in the Mediterranean region (Crivelli, 1995) and can cause taxonomic homogenization (i.e., taxonomic similarity across communities), particularly in the Nearctic and Palearctic regions (Villéger, Blanchet, Beauchard, Oberdorff, & Brosse, 2011, 2015). There is also evidence that only few introduced exotic species (e.g., common carp, *Cyprinus carpio* L.) drive this trend (Toussaint, Beauchard, Oberdorff, Brosse, & Villéger, 2016). There are many studies focusing on the effects of exotic species on native ones (e.g., Milardi et al., 2018); however, large-scale diversity patterns in native and exotic species communities are still understudied, especially in freshwaters (some exceptions: Kuczynski et al., 2017; Leprieur, Olden, Lek, & Brosse, 2009; Maceda-Veiga et al., 2017).

To investigate these patterns, we focused on fish biodiversity in rivers and streams in Northern Italy, one of the most heavily invaded areas in the country. In some stretches of these rivers, the invasion of exotic fish, and a corresponding decline of native species, occurred nearly twenty years ago (Castaldelli, Pluchinotta et al., 2013). Here, we (a) investigated how species richness (i.e., alpha diversity) and the uniqueness of community composition (i.e., beta diversity, LCBD) vary among exotic and native fish species from headwaters to lowland rivers, that is, across stream orders. Secondly, we (b) investigated the relative influence of main water physico-chemical variables on the uniqueness of the community composition at sites (i.e., LCBD). We also (c) examined the variation in exotic and native community within stream orders and studied whether we could relate within stream order variation in communities to the degree of water physico-chemical heterogeneity. Finally, we (d) analysed the species contribution to beta diversity (i.e., SCBD) under the hypothesis that native species might contribute more to beta diversity than exotic ones, which tend to homogenize communities. We also examined if a relationship between species occupancy and species contribution to beta diversity existed.

Our results can help to understand spatial clines in native and exotic species diversity and how these clines respond to different water physico-chemical variables. Such information would in turn be useful to improve management and conservation actions in freshwaters.

2 | METHODS

2.1 | Study area

The study area is located in Northern Italy and includes the largest river basin in Italy, the Po River basin (71,000 km^2). The area hosts more than 17 million of inhabitants and is impacted by agricultural activities and livestock farming. The study region has a

Mediterranean continental climate, with an annual average precipitation of 1,036 mm and a mean air temperature of 12°C. The rivers network considered include the Po River in all its course, the Oglio River, one of the most important left tributaries of the Po River, and the right tributaries in the Emilia-Romagna region. As a reference external to the Po Basin, we included the Brenta River, located on the north-east of the Po Basin, and torrents and rivers south of the Po Basin, until the southernmost border of the Emilia-Romagna region.

In the upland rivers, organic material originating from villages and small towns and livestock farms is the main source of pollution. Conversely, a high degree of urbanization and intensive agriculture characterize the lowland rivers, where high nutrient loads have led to eutrophication (Castaldelli, Soana et al., 2013; Soana, Racchetti, Laini, Bartoli, & Viaroli, 2011). To support agricultural activities, a complex network of drainage canals has been established in the lowlands. This system is completely human-regulated with hydrological management directed to drainage or irrigation supply (Castaldelli, Pluchinotta et al., 2013; Milardi, Chapman, Lanzoni, Long, & Castaldelli, 2017). Overall, a total of 337 sampling sites in 105 watercourses were sampled between 1999 and 2010 and included in this study, covering a wide range of freshwater habitats, different altitudinal zones and environmental conditions (Figure 1). We considered that community turnover would not be a relevant factor in our study, due to the fact that fish communities are typically more temporally stable than other aquatic communities (Korhonen, Soininen, & Hillebrand, 2010). Furthermore, the study area was already in a late invasion stage (Milardi et al., 2018), since loss of native species and exotic invasion occurred mainly prior to 1997 (Castaldelli, Soana et al., 2013), that is, before the data analysed here were collected.

2.2 | Stream surveys

Fish data were collected within a monitoring programme for the compilation of the official Fish Inventories of the Emilia-Romagna region (Emilia-Romagna Region, 2002, 2005, 2008), the Padova province (Padova Province, 2010), the Po River (Po River Water Authority, 2008) and the Oglio River (Oglio River Water Authority, 2016). Fish sampling was performed typically from April to September by electrofishing. In sites of higher water depth and conductivity (e.g., lower stretches of the rivers), electrofishing was combined with the use of nets. For more details on fish sampling methods, see Aschonitis et al. (2018), Gavioli et al. (2018), Milardi et al. (2018).

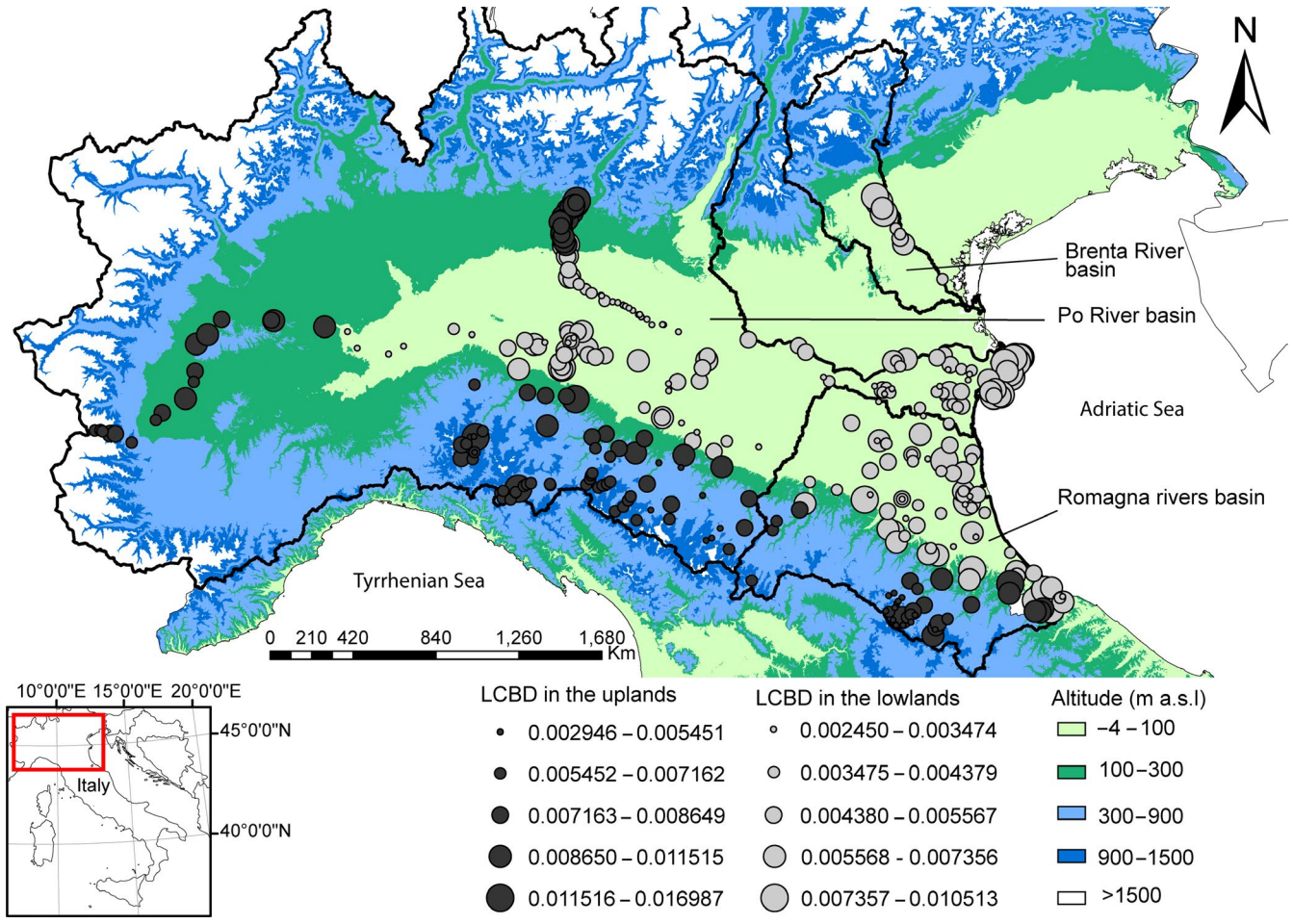

FIGURE 1 Map of sampling sites in the Northern Italy, altitudinal gradient and Local Contribution to Beta Diversity for upland (dark grey circles) and lowland sites (light grey circles) calculated for the total fish community. Po River basin, Brenta River basin and Romagna rivers basin are shown

Fish species were classified according to Kottelat and Freyhof (2007), taking into account recent taxonomic determinations and common names as listed in FishBase (Froese & Pauly, 2017). Each species was categorized as native or exotic: a species was considered as native when naturally present in Italian watercourses, and as exotic when introduced by humans, irrespective of the time elapsed since the introduction. Fish species abundance was expressed using Moyle classes (Moyle & Nichols, 1973) ranging from 1 (lower abundance, 1–2 individuals per site) to 5 (higher abundance, more than 50 individuals per site). Hybrid specimens or uncertain species were excluded from this study in order to avoid taxonomic asymmetries.

Typically, in European rivers, fish communities change from Salmonidae to Cyprinidae dominated, along an altitude gradient, from headwaters to large rivers at low elevation (Aarts & Nienhuis, 2003). Taking into account such community shifts, study sites were divided into two groups: lowland sites (sites below 100 m above sea level) and upland sites (sites above 100 m above sea level). This limit is not absolute and it is not a strong physical barrier for fish species, but it was chosen based on earlier studies in the region (Aschonitis et al., 2018; Milardi et al., 2018) and separate typical lowland impacted environments from the less impacted ones, located in the uplands.

Water physico-chemical sampling was performed with standard methods in proximity to the fish sampling sites by Regional Environmental Protection Agency (ARPA) for Po River, Brenta River and Emilia-Romagna rivers and by Oglio River Water Authority for the Oglio River. Eight water physico-chemical variables were included as follows: water temperature (°C), electrical conductivity (μS/cm), chemical oxygen demand (COD [O_2 mg L^{-1}]), biological oxygen demand (BOD_5 [O_2 mg L^{-1}]), total suspended solids (mg/L), total phosphorus (P mg L^{-1}), ammonia (N mg L^{-1}) and nitrate nitrogen (N mg L^{-1}).

2.3 | Stream order analysis

The stream order of each sampling site was calculated from Digital Elevation Model (DEM) data (ISPRA, Italian Institute for Environmental Protection and Research) through the ArcGIS 10.1 software. In order to harmonize the elevation model, the DEM layer was first resampled into 10 m pixel size. Then, using the Hydrology Spatial Analyst Tool, the flow direction and the flow accumulation based on DEM layer were calculated. Finally, for the entire river network generated by flow accumulation, the stream order with the Strahler method (Strahler, 1957) was calculated. This procedure resulted reliable for upland streams, while in the lowland, it was less accurate possibly due to the fact that in the lowlands, the flow direction and magnitude have been modified by humans. The Strahler stream order was thus manually checked and revised when necessary in lowland rivers and streams.

In order to balance the number of rivers sampled in each Strahler stream order, rivers were grouped into four classes based on stream order: class 1—rivers with 1 and 2 Strahler stream order, class 2—rivers with 3 and 4 stream order, class 3—rivers with 5 and 6 stream order and class 4—rivers with Strahler stream order higher than 6. As the drainage and irrigation canals located in lowlands could not be assigned into any natural class, they were assigned into a separate class called "Drainage."

Overall, in the uplands, six sampling sites were included in stream order class 1, 41 in stream order class 2, 55 in stream order class 3, 6 in stream order class 4 and no sites were sampled in drainage canals. In the lowlands, no sampling sites were included in the first stream order class, 17 were included in stream order class 2, 53 in stream order class 3, 94 in the stream order class 4 and 40 in the drainage canals.

2.4 | Statistical analysis

All statistical analyses were performed for lowland (204 sampling sites below 100 m of altitude) and upland (133 sampling sites above 100 m of altitude) sites separately, taking also into account the distinction between exotic and native fish species.

2.4.1 | Species richness and local contribution to beta diversity in exotic and native fish species

To study the uniqueness of fish community composition across sites, the Local Contribution to Beta Diversity (LCBD) was calculated for each sampling site using the *beta.div* function in "adespatial" R package (Dray et al., 2018) based on Legendre and De Cáceres (2013). This method calculates the Total Beta Diversity (BD_{Total}) from the total variance of a site by species community table. The LCBD was derived by partitioning the BD_{Total} into the local contributions, and the sum of the LCBDs for all sites is equal to 1. For this metric, higher values of LCBD of a site indicate an unusual species composition compared with the average community in the data. From an ecological point of view, the LCBD values represent the degree of uniqueness of the sampling units in terms of community composition (Legendre & De Cáceres, 2013).

To investigate how LCBD and richness varies across stream order classes, the Kruskal–Wallis (KW) test (R function *kruskal.test*) was applied. The choice of Kruskal–Wallis test was due to the fact that data did not meet all assumptions of ANOVA, tested with *ad.test* function in "nortest" package (Gross & Ligges, 2015).

2.4.2 | Relative influence of main water physico-chemical variables on the local contribution to beta diversity

A machine learning method, Boosted Regression Trees analysis (BRT; Elith, Leathwick, & Hastie, 2008), was used to investigate how LCBD was influenced by water physico-chemical variables. BRT has been considered to be an efficient method to describe any nonlinear relationships between variables (e.g., thresholds) and it automatically incorporates interactions between variables. This approach differs from traditional regression methods as BRT analysis combines together a large number of simple tree models using the boosting technique to improve the predictive performance. BRT analysis further calculates the relative influence of predictors on response variable. The effect of predictors is showed through the fitted functions

that provide a useful basis for interpretation, although they are not perfect representation in case of strong interactions between predictors (Elith et al., 2008). BRT was performed with Gaussian distribution, bag fraction of 0.75 and shrinkage of 0.001 in the R software package "gbm" (Ridgeway & Southworth, 2017).

2.4.3 | Variation in exotic and native community dispersion among and within stream orders

In order to investigate the degree to which there is community structural variation within a stream order class, a test of homogeneity of dispersion (PERMDISP) was used (Anderson, 2006; Anderson, Ellingsen, & McArdle, 2006) with a function *betadisper* in the "vegan" R package (Oksanen et al., 2017). Through the average dissimilarity from individual observations to their group centroid, this test calculates the degree of dispersion, that is beta diversity (when based on presence–absence data) and the community structural variation (when based on abundance data; Anderson et al., 2006; Heino et al., 2013) within stream order and test if it differs among stream orders. The PERMDISP analysis was run using Gower dissimilarities on fish abundance data and Sørensen dissimilarity on presence/absence data. Moreover, we also investigated the degree of water physico-chemical dispersion within stream order classes using Euclidian distances. A permutation test with 999 permutations (*permutest* function) was used to compare the degree of within group dispersions among groups. A linear regression analysis was used to test the null hypothesis of no relationship between the distance of centroid based on abundance data (i.e., communities structural variation) and the distance to centroid of water physico-chemical variables (i.e., water physico-chemical heterogeneity) across sites (Heino et al., 2013).

2.4.4 | Differences in species contribution to beta diversity between native and exotic species and the relationship with species occupancy

We calculated the Species Contribution to Beta Diversity (SCBD) that shows the degree of variation of a species across the considered area (Legendre & De Cáceres, 2013). It can be considered as a measure of the relative importance of each species in affecting beta diversity (Heino & Grönroos, 2017). Linear regression was used to investigate the relationship between the SCBD values and the number of sites occupied for each species and the Kruskal–Wallis test was used to investigate difference in SCDB values between the lowlands and uplands.

All statistical analysis was performed in R software, version 3.4.3 (R Core Team, 2017).

3 | RESULTS

A total of 60 fish species were observed in the study area, with 38 native and 22 exotic species. In the upland sites, fish community was composed of 24 native species and 11 exotic species, whereas in the lowland sites, 38 native and 22 exotic species were found (Supporting information Table S1).

Minimum, maximum, averages and standard deviations of water physico-chemical variables and altitude for lowland and upland sites are reported in Supporting information Appendix S1: Appendix A. Variation of water physico-chemical variables along stream order classes are shown in Supporting information Appendix S1: Appendix B. In summary, lowland sites showed the highest anthropogenic pollution, with the highest values of ammonia and nitrate nitrogen, chemical oxygen demand (COD), biological oxygen demand (BOD_5) and total phosphorus. Also, electrical conductivity, mainly due to brackish waters, and total suspended solids were higher in the lowland sites than upland sites. Due to the altitudinal gradient, the lowest water temperatures were detected in the upland sites.

3.1 | Species richness and local contribution to beta diversity in exotic and native fish species

Exotic fish species richness was higher in lowland sites than upland sites, where only few exotic species were recorded (Figure 2). The exotic species richness showed significant differences among stream order classes in the lowlands (KW $\chi^2 = 53.7$, $df = 3$, $p < 0.001$) and in the uplands (KW $\chi^2 = 71.2$, $df = 3$, $p < 0.001$) with a positive trend towards higher stream orders (Figure 2a, b). Native species showed significant differences among stream order classes in both lowlands (KW $\chi^2 = 54.0$, $df = 3$, $p < 0.001$) and uplands (KW $\chi^2 = 71.2$, $df = 3$, $p < 0.001$). In the lowlands, native richness peaked in stream order class 3 and was lowest in drainage canals, whereas in the uplands richness was highest in stream order class 4 and lowest in class 1 (Figure 2a, b).

Considering all fish species, BD_{total} for lowland and upland sites were 0.631 and 0.607, respectively. The distribution of LCBD values considering all species is shown in Figure 1. The highest values of LCBD in the lowland sites occurred in the Po River Delta and in South-East area of Emilia-Romagna region. In upland sites, LCBDs showed a high spatial variability across the studied area. According to the Kruskal–Wallis test, LCBD values did not show significant differences among stream order classes in the lowlands considering native species (Figure 3a; KW $\chi^2 = 1.7$, $df = 3$, $p > 0.05$). Whereas considering exotic species, LCBD values showed a significant difference among stream order classes (KW $\chi^2 = 9.0$, $df = 3$, $p < 0.05$) more evident between the stream order class 3 and drainage canals class (Figure 3a). In the uplands, LCDB values showed significant differences considering both native (Figure 3b; KW $\chi^2 = 24.7$, $df = 3$, $p < 0.001$) and exotic species (Figure 3b; KW $\chi^2 = 65.6$, $df = 3$, $p < 0.001$) along stream order classes, reaching the highest values in large rivers.

3.2 | Relative influence of main water physico-chemical variables on the local contribution to beta diversity

According to BRT analysis, the total suspended solids and the total phosphorus were retained as the most important factor affecting

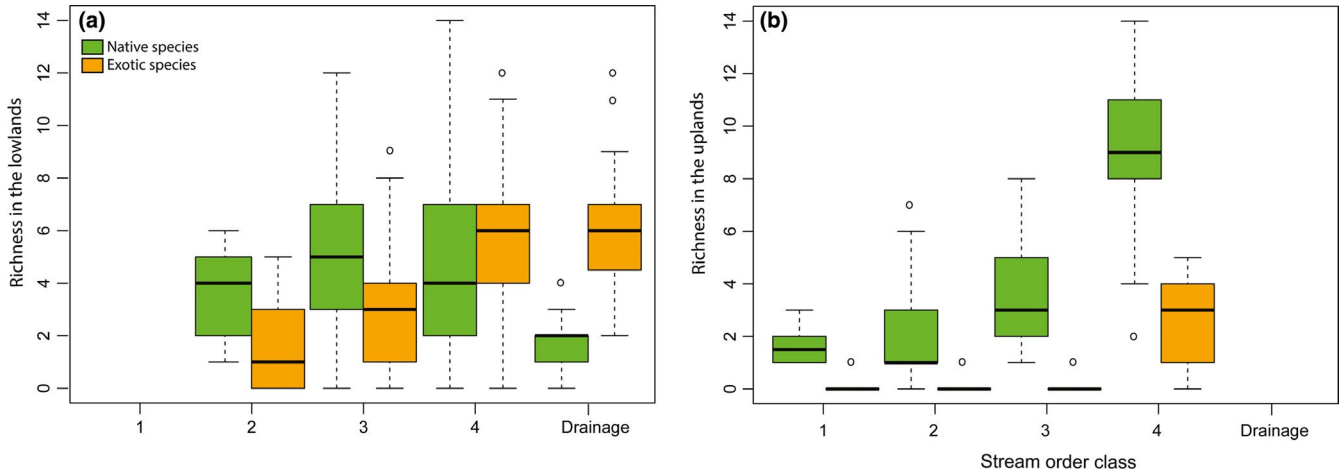

FIGURE 2 Boxplots representing the values of exotic (orange) and native (green) fish species richness in the lowlands (a) and uplands (b) along stream order classes

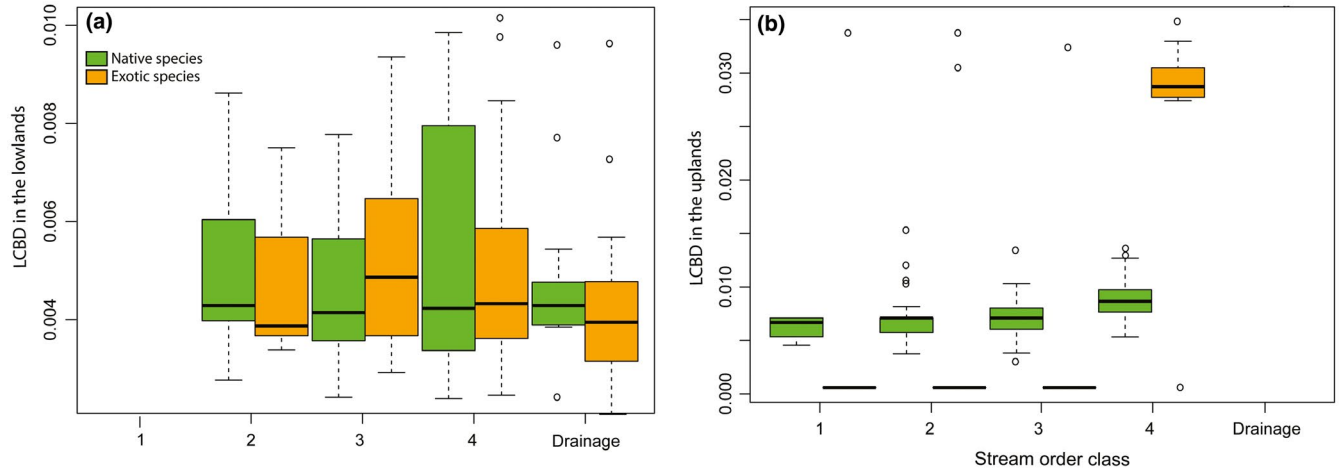

FIGURE 3 Boxplots representing Local Contribution to Beta Diversity (LCBD) values for exotic (orange) and native (green) fish species along stream order classes in the lowlands (a) and uplands (b)

LCBD values for both exotic and native species in the lowlands and in the uplands, respectively (Figure 4). As evident in the fitted functions, these predictors showed negative relationships with respective LCBD. The chemical oxygen demand (COD) was the second most important predictor among native species, for both lowland and upland sites, and it showed a positive relationship with LCBD. Among exotic species, a second important factor was total phosphorus in lowland sites, having a negative influence on LCBD at low phosphorus levels. In upland sites, nitrate nitrogen had the highest influence being positively related with LCBD, having a clear threshold above which LCBD notably rises.

3.3 | Variation in exotic and native community dispersion among and within stream orders

According to PERMDISP analyses, within stream order dispersion varied significantly among stream order classes (Figure 5) for exotic species both in lowlands ($F_{(3, 200)} = 26.8$, $p < 0.01$,) and uplands ($F_{(3, 129)} = 119.3$, $p < 0.01$,), but also for native species in the lowlands ($F_{(3, 200)} = 20.2$, $p < 0.01$) and uplands ($F_{(3, 129)} = 61.4$, $p < 0.014$). Based on the pairwise comparisons, within stream order dispersion differed significantly in larger rivers regardless to altitudinal zones and in drainage canals network. Stream orders did not differ in their water physico-chemical heterogeneity (Supporting information Appendix S1: Appendix C) either in the lowlands ($F_{(3, 200)} = 0.4$, $p > 0.05$) or in the uplands ($F_{(3, 129)} = 0.5$, $p > 0.05$). According to linear regression analysis, within stream water physico-chemical heterogeneity had no significant relationship with community dispersion either for native and exotic species in the uplands ($R^2 = 0.004$, $p > 0.05$; $R^2 = 0.014$, $p > 0.05$, respectively) or for exotic ones in the lowlands ($R^2 = 0.0001$, $p > 0.05$). However, a weak but significant relationship was found for native species in the lowlands ($R^2 = 0.024$, $p < 0.05$).

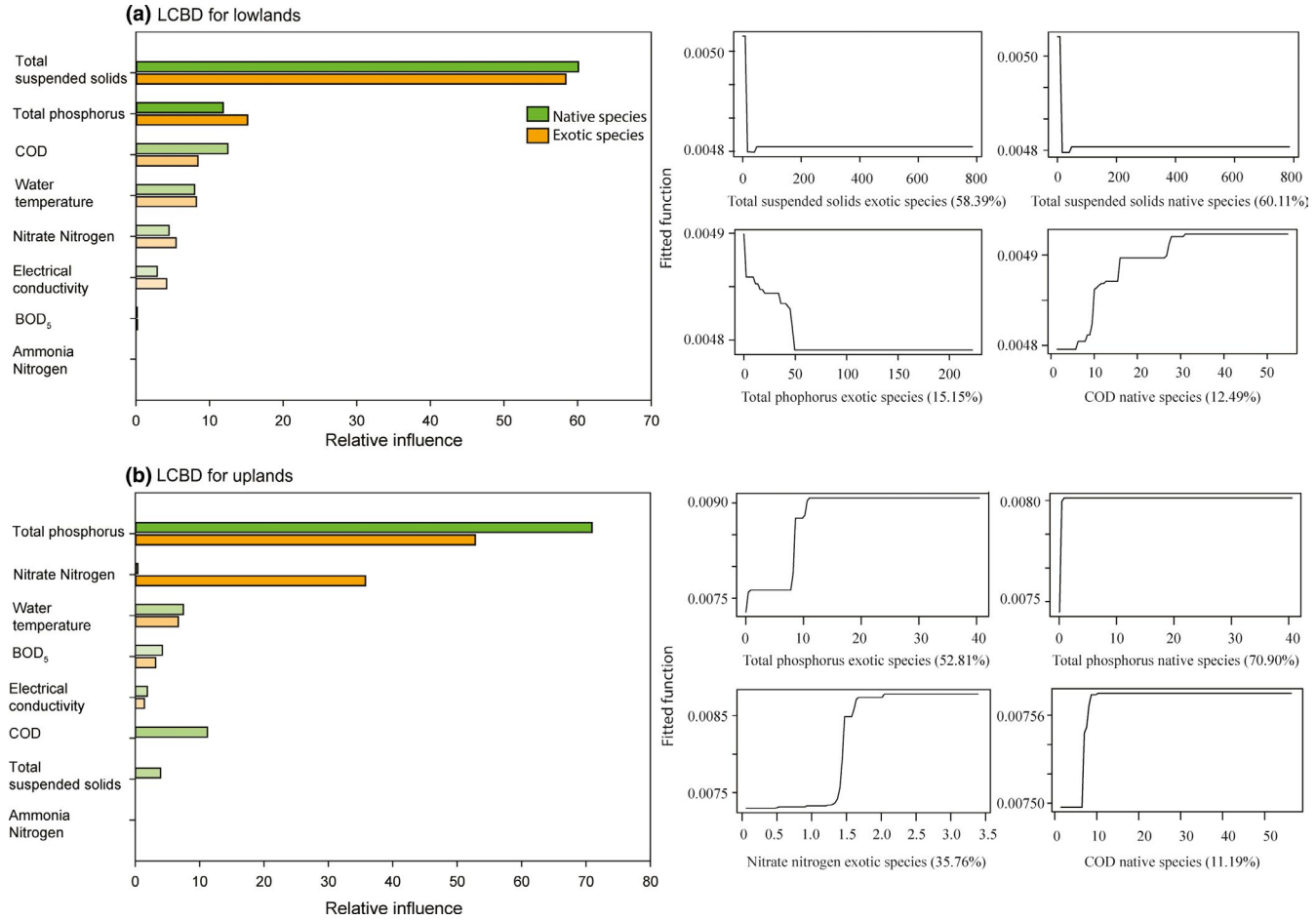

FIGURE 4 Boosted Regression Tree summary showing the relative influence of water physico-chemical variables on Local Contribution to Beta Diversity (LCBD) values for lowland (a) and upland (b) sites. The curves of fitted function for the most important variables are also shown in the panels on the right. COD: chemical oxygen demand

3.4 | Differences in species contribution to beta diversity between native and exotic species and the relationship with species occupancy

SCBD showed a linear positive relationship with the number of sites occupied for each species (Figure 6, both for exotic (R^2 = 0.91, p < 0.001) and native species (R^2 = 0.90, p < 0.001) in the lowland sites (Figure 6a) and in the upland sites (Figure 6b; R^2 = 0.74, p < 0.001 for native species; R^2 = 0.31, p < 0.001 for exotic species). SCBD values and species occupancy for each species are given in Supporting information Appendix S1: Appendix D. According to the Kruskal–Wallis test, no differences were found in SCBD values between exotic and native communities in the lowlands sites (KW χ^2 = 2.4, df = 1, p > 0.05), whereas in the upland sites SCBD values were higher for native species than exotic ones (KW χ^2 = 8.3, df = 1, p < 0.01).

4 | DISCUSSION

Large-scale diversity studies focusing simultaneously on exotic and native species diversity in freshwater ecosystems are still relatively rare, although exotic species may play a strong role in native species diversity loss. This study investigated diversity patterns and their drivers among exotic and native stream fish species.

4.1 | Species richness and local contribution to beta diversity in exotic and native fish species

An increase of species richness from headwaters to lowland rivers was previously found not only in fish (Beecher, Dott, & Fernau, 1988; Chea, Lek, Ngor, & Grenouillet, 2017) but also in other taxa such as macroinvertebrates and diatoms (Finn, Bonada, Múrria, & Hughes, 2011; Stenger-Kovács, Tóth, Tóth, Hajnal, & Padisák, 2014) suggesting a general diversity pattern. Different mechanisms have been proposed to drive this pattern, including water temperature, river morphology (e.g., depth and width) and habitat diversity (Allan & Castillo, 2007). In our study, only exotic species richness increased with stream order classes with the highest exotic richness in the largest rivers and drainage canals network. In contrast, native richness showed an increase across stream order only in the uplands, whereas in the lowlands, native species richness decreased in large rivers and drainage

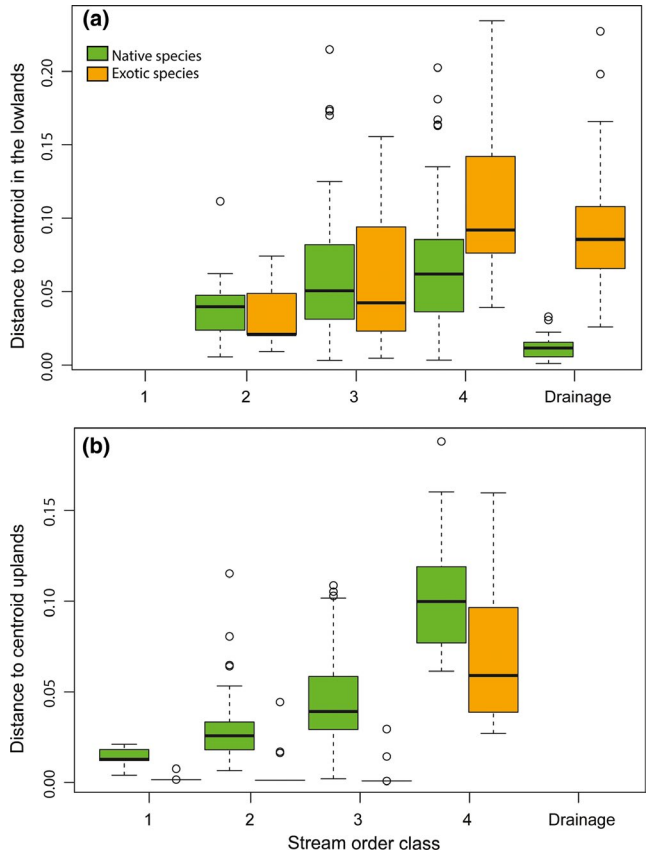

FIGURE 5 Boxplots showing mean distance to centroids along stream order classes, based on Gower dissimilarities of native (green) and exotic (orange) fish species in the lowlands (a) and in the uplands (b)

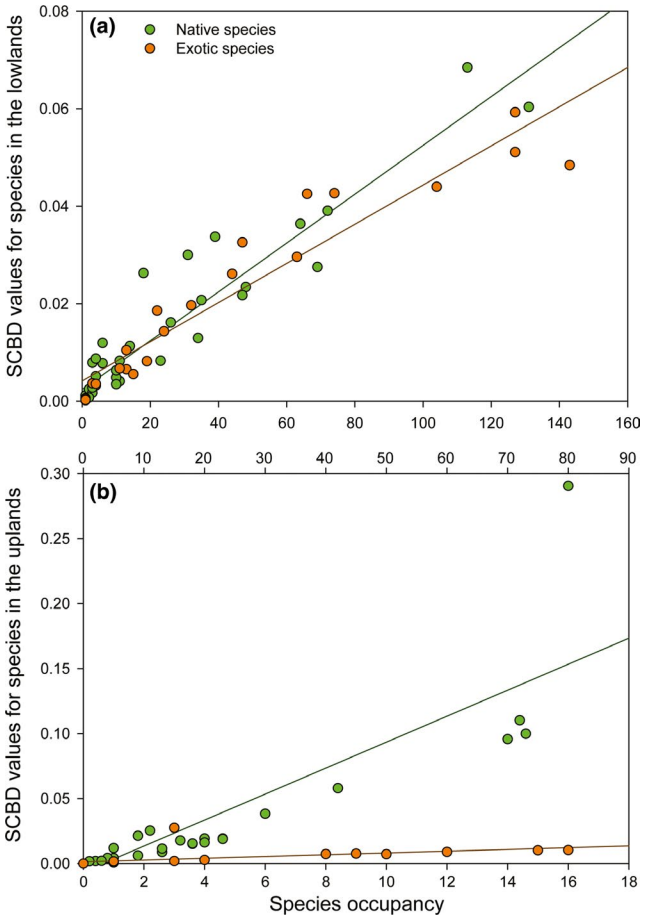

FIGURE 6 Relationship between Species Contribution to Beta Diversity (SCBD) and fish species occupancy (number of sites) for exotic (orange points) and native (green points) species, in the lowland (a) and the upland (b) sites. Please note that scales in occupancy for native and exotic species in panel b) are different for exotic (down) and native (up) species

canals network. Anthropogenic disturbance (e.g., pollution, river modifications and flow regulation) could partly explain low native species richness in lowland rivers, and particularly in the artificial drainage network, but also past exotic species invasions could have played a central role in shaping this distribution. In fact, exotic species have pushed most lowlands native species on the edge of local extinction in several sites and displaced most of them on the boundary of their natural distribution to the highest reach of the rivers (Milardi et al., 2018). However, upstream rivers cannot provide suitable habitats for all such native species and cannot completely compensate the loss of native species of the lowlands.

The decline in native species richness was more evident in drainage canals network where direct effects (e.g., predation and competition) and indirect effects (e.g., changes in water quality) of some successful exotic invaders (e.g., *Silurus glanis and Cyprinus carpio*) were amplified due to the lower habitat complexity (Castaldelli, Pluchinotta et al., 2013).

Conversely to richness patterns, LCBD did not show clear differences among stream order classes in the lowland sites for either native or exotic species, suggesting that fish communities in different stream orders had typically similar degree of uniqueness. This result indicated a similar community composition across sites in the lowlands, probably driven by the most widespread exotic species such as the common carp or the crucian carp (*Carassius* spp.). These two species can also promote homogenization in communities especially in Palearctic regions (Toussaint et al., 2016; Villéger, Blanchet, Beauchard, Oberdorff, & Brosse, 2011). Upland sites (high stream order class) contributed strongly to beta diversity of exotic and native species, suggesting that large rivers at higher elevations could provide regionally unique habitats and conditions. Interestingly, high exotic species LCBD values in large upland rivers can be the result of an early invasion process from widespread exotic communities in the lowlands (Milardi et al., 2018) and thus underline a need for conservation and possibly restoration of such sites (Legendre & De Cáceres, 2013). These results suggest that not only headwater streams require conservation attention for native fish species, as suggested in other studies (Matthews, 1986; Paller, 1994), but that large rivers in the uplands can also contribute to regional diversity by harbouring unique native species communities.

4.2 | Relative influence of main water physico-chemical variables on the local contribution to beta diversity

Different water physico-chemical variables were proven important for LCBD in lowland versus upland sites when considering both exotic and native species. The large importance of total suspended solids in explaining LCBD (with negative relationship) reflects not only anthropogenic effects but also the effects of exotic ecosystem-engineering species such as crucian or common carp. In fact, these species can increase water turbidity through the resuspension of sediments while feeding, in turn causing a phytoplankton biomass increase and loss of submerged vegetation, while being able to tolerate high turbidity themselves (Crivelli, 1995). As a consequence, fish community tend to change reflecting this environmental shift, with for example a loss of clear water species with the water turbidity rise.

In upland sites, LCBD was mainly driven by total phosphorus, suggesting a strong role of nutrients on beta diversity patterns. Nutrients can affect beta diversity promoting the presence of highly tolerant species and negatively affecting the most sensitive species. Similar results were found also in Finnish lakes, where species richness of eutrophication-tolerant species increased towards higher nutrient loads (Olin et al., 2002).

Other authors suggested a strong influence of morphological factors (e.g., water depth, width, flow conditions or substratum typology) on diversity patterns, such as substrate features on diatoms (Jyrkänkallio-Mikkola, Heino, & Soininen, 2016), macroinvertebrates (Heino et al., 2013) and fish (D'Ambrosio, Williams, Witter, & Ward, 2009). Unfortunately, in our dataset, data on morphological features were not available, and the investigation of their role in affecting LCBD was not possible. However, supporting the importance of water chemistry, also Maceda-Veiga et al. (2017) recently found that salinization and nutrient pollution (such as nitrate, nitrite, phosphate supply) constitute one of the major threats to native fish, in addition to hydrological features.

4.3 | Variation in exotic and native community dispersion among and within stream orders

The degree of water physico-chemical heterogeneity did not vary among stream order classes either in uplands or in the lowlands, suggesting that water conditions do not differ among stream order classes. We also did not find a relationship between community dispersion and heterogeneity in water physico-chemical variables (except for native communities in the lowlands). The absence of such relationships was also found by Heino et al. (2013) in stream macroinvertebrate communities and by Jyrkänkallio-Mikkola et al. (2016) for diatoms. Different explanations already proposed for such a pattern could also be applicable here: (a) fish species distributions may not have been related only to water conditions but also to dispersal processes, (b) patterns are difficult to see at the community level due to the species-specific responses and (c) the lack of important habitat descriptors such as river morphology (Heino et al., 2013). Although only the water physico-chemical descriptors were considered in this study, we expect that water physico-chemical patterns might reflect also other, more general, stream alterations due for example to agriculture or farm animals (Allan & Castillo, 2007). Thus, we conclude that the degree of community dispersions does not strongly depend on the level of water physico-chemical heterogeneity within stream order classes. The only exception was native species communities in the lowlands, which showed a weak relationship with water physico-chemical heterogeneity, perhaps indicating their somewhat higher sensitivity to water quality variations due to anthropogenic pressures or to exotic fish species presence as discussed above.

4.4 | Differences in species contribution to beta diversity between native and exotic species and the relationship with species occupancy

As we hypothesized, native species had higher SCBD values than exotic species, but only in the uplands. The fact that SCBD values did not often differ between native and exotic species in the lowlands could be the result of simplified native communities, composed by the few native species most resilient to the invasion process, as previously suggested by other studies in the same area (Lanzoni, Milardi, Aschonitis, Fano, & Castaldelli, 2018; Milardi et al., 2018). It may also indicate that exotic species communities are spatially structured, with different species dominating communities across sites (Clavero & García-Berthou, 2006). One more reason could be the positive relationship between SCBD and the species occupancy, suggesting that the most widespread fish species (which are often exotic species, too) can strongly affect beta diversity. For example, competition and predation mechanisms as well as the fact that exotic species are able to change environmental conditions can concur to exclude native species from a fish community. However, the expected positive relationship between abundance based SCBD values and species occupancy was previously found also in stream insects by Heino and Grönroos (2017) suggesting that species with high SCBD values are expected to have relatively high local abundance and high sites occupancy. Our results also confirm the predictability of SCBD values from species occupancy and abundance (Heino & Grönroos, 2017; da Silva, 2018).

However, perhaps counterintuitively, it is not always true that species with high SCBD (i.e., high contribution to beta diversity) are important to preserve diversity when exotic or native status was considered. For example, in lowland sites, the most widespread exotic species such as the stone moroko (*Pseudorasbora parva*), the crucian, carp and the common carp showed high SCBD but, due to the homogenization effect (Toussaint et al., 2016) and their ability to modify the environment (Breukelaar, Lammens, Breteler, & Tatrai, 1994; Chumchal, Nowlin, & Drenner, 2005; Alain J. Crivelli, 1983), they can negatively affect native species diversity. Of consequences, the high SCBD values can help to

identify the most abundant and widespread exotic species which could have negative effect on native communities. Likewise, high SCBD values in native species can identify species that not need conservation measures due to the high abundance and wide distribution, such as the chub (*Squalius squalus*) or the Italian bleak (*Alburnus alborella*). Contrarily, low SCBD values can identify rare native species, that for the low abundance and restricted distribution that require major conservation measures such as the Italian nase (*Chondrostoma soetta*), and the South European nase (*Protochondrostoma genei*), classified as endangered by IUCN and included in the Habitat Directive (Annex II). It is also possible that some low SCBD values were due to the low sites occupancy of species at the edge of their distribution such as the rainbow trout, *Oncorhynchus mykiss*, in the lowlands or the Eastern mosquitofish, *Gambusia holbrooki*, in the uplands.

Taking into account these aspects, these analysis outputs required accurate consideration as to the geographical range and the exotic or native species status. We encourage future research in this field to update the information available and to better understand the major drives of it.

5 | CONCLUSIONS

Due to the loss of native freshwater biodiversity worldwide (Strayer & Dudgeon, 2010), the need for the identification of priority areas for conservation (Hermoso, Clavero, & Kennard, 2012) and the limited conservation resources available; there are three main implications for future conservation strategies found in this paper: (a) not only headwaters require conservation measures but also large upland rivers are important in contributing to native fish diversity. These systems resulted in a low exotic species presence, promoting zones with high native diversity. (b) In upland sites, native species showed the highest contribution to beta diversity, but this pattern was not found in lowland sites, which shows the importance of protecting native communities in upland sites, while suggesting a general homogenization process in the lowland communities. (c) Some rare native species that are restricted to few sites can show low contribution to beta diversity, but such species may still need conservation actions due to their risk of local extinctions. This suggests to interpret the results of SCBD carefully, because the abundance of rare species is typically underestimated.

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DATA ACCESSIBILITY

Fish data used in this study are shown in Supporting information Table S1. Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.83g8j8f

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BIOSKETCH

The authors have a background in species diversity distributions (J.S.), fish and invasion ecology (A.G., G.C., M.M.) as well as general ecology (E.A.F.). These different research lines were joined to investigate the spatial distribution of fish species and its drivers, considering the exotic/native species status.

Author contributions: J.S. and G.C. conceived the idea, A.G. collected the dataset and analysed the data, A.G. and J.S. led manuscript writing, M.M., G.C and E.A.F provided major input on the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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